

THE UPPER FOSSIL FAUNA OF THE HENSCHKE FOSSIL CAVE, NARACOORTE, SOUTH AUSTRALIA

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The Henschke Fossil Cave was discovered in a quarry near Naracoorte in 1969. The fossiliferous silt was excavated systematically from the upper levels of the cave during the next eleven years. The resulting fossils from each designated area and arbitrary level were analysed for species, and minimum numbers calculated. Relative abundance of each species was calculated for each level in the combined central areas of the deposit, and is presented graphically. Opposing trends of relative abundance are revealed for some species, and might reflect environmental changes. Age determinations on charcoal indicate that this part of the cave filled between 32,000 and 40,000 years ago, before becoming sealed. Interpreted environmental changes from a wetter, denser, forest to drier, more open, shrubby woodland, agree with climatic and vegetational data obtained elsewhere in the region. Comparisons are made with the fauna of the nearby Victoria Fossil Cave.

□ Pleistocene, Henschke Fossil Cave, taphonomy, Anura, Lepidosauria, Chelonia, Aves, Monotremata, Marsupialia, Eutheria.

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The Henschke Fossil Cave was discovered in 1969 as the result of quarry operations on the outskirts of Naracoorte, South Australia (Fig. 1, 2a, 2b) and was reported to the South Australia Museum.

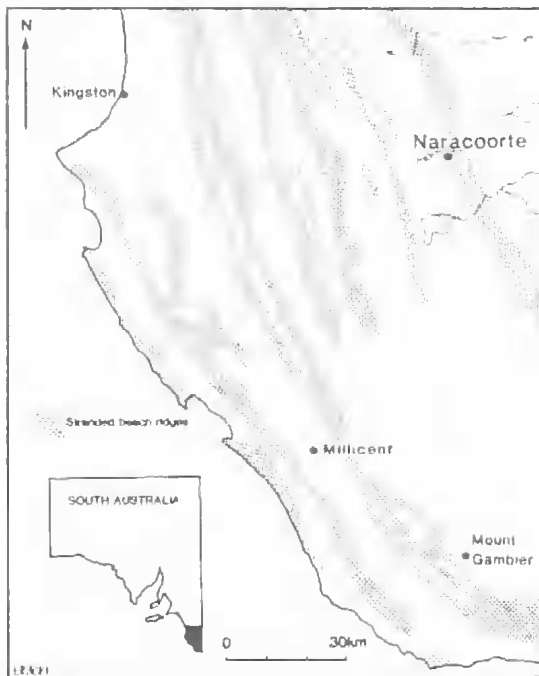


FIG. 1. Locality map. SE South Australia with major towns and stranded beach ridges.

The southeastern region of South Australia is underlain by the Oligocene-Miocene Gambier Limestone, and in the Naracoorte region, this is capped by the resistant early-mid Miocene Naracoorte Limestone Member of the Gambier Limestone (Ludbrook, 1961). Following regional uplift in the later Miocene, when karst features were developed (Wells et al., 1984), there was a brief period of inundation during the Pliocene. Pleistocene sea-level fluctuations, combined with steady uplift, left a distinctive signature of stranded beach ridges on the landscape (Hossfeld, 1950; Sprigg, 1952, 1959; Cook et al., 1977; Idnum & Cook, 1980). In the Naracoorte area caves tend to be associated with these aeolian ridges, particularly the Naracoorte East Range, which sits upon a scarp of Naracoorte and Gambier Limestones associated with the buried Kanawinka Fault. The present caves are apparently elaborations on exhumed Miocene karst features, although no trace of cave sediment older than Late Pleistocene has been recognised.

The several quarries around Naracoorte owe their existence to uplift along the Kanawinka fault; all show karst features - "pot-holes" filled with Pliocene Parilla Sand (Wells et al., 1984) or small caves (e.g. Daily, 1960). In 1969, Henschke's Quarry broke into another small cave. At the far end of the cave a few bones of extinct species of

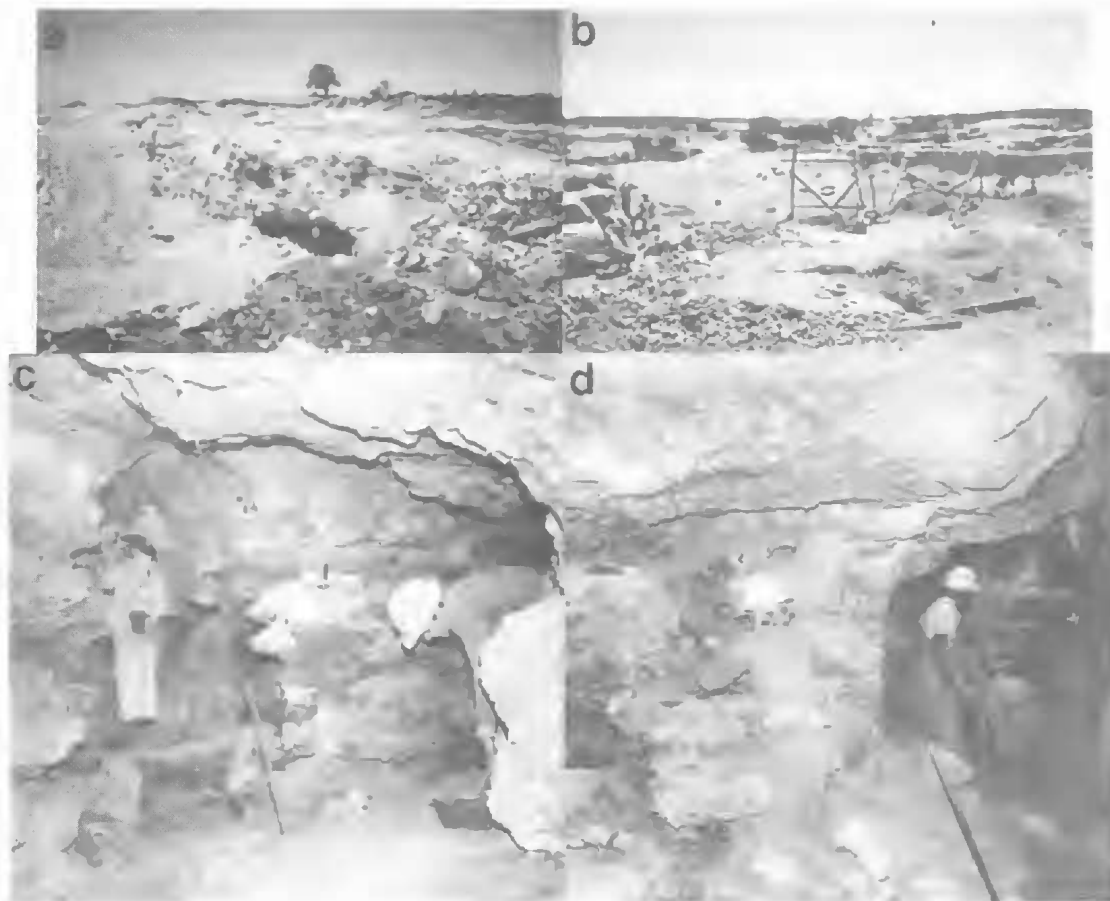


FIG. 2. a) View to SE along the line of the Henschke Fossil Cave, showing a figure in the second entrance and the cap rock of Naracoorte Limestone. b) View to NW along the line of the Henschke Fossil Cave, with the excavated natural entrance in foreground, and Naracoorte in the background separated by a marshy interdune valley. c) Main passage, looking NW from the natural entrance. Silt filled this passage almost to the top of the photo. d) View from the main passage to the natural entrance, which was used as the major means of access during later phases of the excavation.

marsupials lay on the surface of a deep, red silt deposit.

METHODS

Excavation techniques evolved during the eleven years of work in the cave. Initially, working from a point where the quarry had accidentally broken in a second time, digging proceeded along the tunnel in 1 m areas. A centre-line was established in this part of the tunnel after the cave had been surveyed by Mr F.W. Aslin. Notable finds were plotted relative to this line as no distinctive bedding could be discerned. The survey showed that an access hole could be dug from the surface through

about 2 m of roof rock to a blind shaft almost directly above the farthestmost open area of silt. It also showed that just beyond the perceptible limit of the tunnel there was a large shallow surface depression.

After about 5 m of the tunnel had been excavated, operations moved to a point below the access shaft, and an area (A1, see Fig. 3) 0.9 m² was dug out in arbitrary 7.5 cm layers. The silt was brought to the surface and sieved through a garden sieve (6 mm mesh), all teeth, jaws and unusual bones being kept. Analysis showed no perceptible sedimentary layering, nor any obvious faunal differences through the 1.8 m depth of the pit, which ended in broken rock. This may have been due to the small area being sampled. The

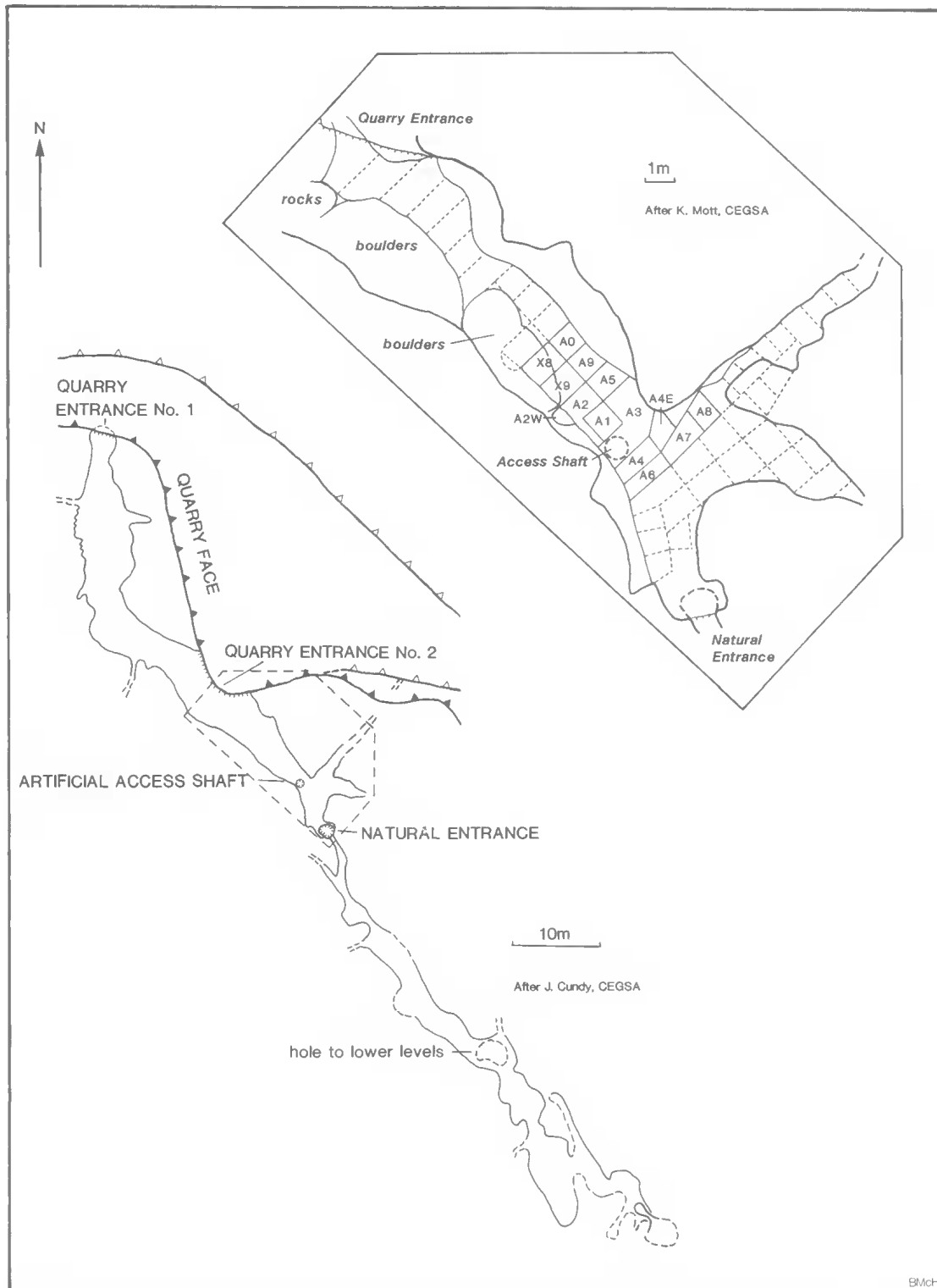


FIG. 3. Henschke Fossil Cave. Plan of upper cave, with detail of excavated area. Census areas designated.

excavation was therefore extended laterally in discrete areas of about 1 m², in layers 15 cm thick. In this way most of the tunnel and its accessible offshoots were excavated. The surface depression was considered to be an infilled entrance, and excavation eventually proved this, disclosing a pot hole about 1 m X 1.5 m X 3 m deep. The tunnel was found to continue to the SE for another 60 m, but no bones were seen on the surface. The cave was resurveyed and mapped by the Cave Exploration Group of South Australia. (Fig. 3).

It was soon realised that small items were being overlooked in the sieves because they were coated with mud. Therefore, the concentrate in the sieves was kept, dried and later screen-washed through flymesh. Occasional unsieved samples were also screen-washed to check for particularly small specimens. The identifiable teeth and bones from each layer of each area were kept separate for later analysis, and also to facilitate possible correlation of associated elements. Charcoal was collected wherever it was in sizeable lumps or concentrations, and two samples were eventually submitted for dating.

Subsequently, teeth and jaws, and bones of some taxa, were identified as closely as possible. Minimum numbers of individuals of each mammal taxon in a layer sample were calculated by pairing jaws, and counting them *plus* the excess. If represented only by isolated teeth, a species was recorded as "present". Ultimately, census was done for an area of about 7 m along the tunnel (Fig. 3). Gross numbers for each 15 cm layer were added, percentages of the total identifiable mammal fauna calculated and the results tabulated.

All specimens are housed in the Palaeontological collections of the South Australian Museum, prefix SAM P.

THE CAVE

Being in a working quarry, it was inevitable that the cave would be destroyed. However, through the good offices of the owners, Henschke Industries, this was delayed until 1981 when our excavations had been completed as far as was practicable.

As first seen, the cave was a simple tunnel about 50 m long trending roughly NW-SE, with a southward dog-leg bend about halfway along. The floor of the first half was littered with large fallen boulders. At about the bend, reddish fossiliferous silt began to appear below these boulders, which increased in size but disappeared after another 8 m. The silt floor gradually rose towards the far end

which narrowed impassably and pinched out. A narrow side passage extended to the east.

On excavation it was found the silt reached a maximum depth of over 3 m, near the natural entrance pothole. Here the cave expanded laterally so that the entrance was bell-shaped, and, therefore, almost escape-proof; a natural pit-fall trap. In this, the cave resembles McEachern's Cave (Wakefield, 1967), but differs in having been sealed before the Holocene.

The sediment is primarily a red-brown silty sand, with a small but annoyingly appreciable clay component (which continually caused the sieves to clog), and occasional coarse sand. It is apparently derived from the Pleistocene Bridgewater Formation, an aeolian sand forming the beach dune ridges such as the East Naracoorte Range. (A fortuitous rainstorm during the excavation of the natural entrance showed how readily the cave sediment could accumulate: sheet wash from a relatively small area — less than one hectare — of gently sloping hillside emplaced more than a metre of sediment in the pit). Rare laterite pebbles suggest also some reworking of the Pliocene Parilla Sands (Firman, 1967). Rockdust and fragments from the cave roof formed a variable component of the sediment. The lowest parts of the deposit tended to be gritty and rather greenish-yellow, apparently with breakdown products from the limestone.

Although a large longitudinal section of the sediment was cleared, no bedding planes of more than 1 m could be seen, in contrast to McEachern's Cave (Wakefield, 1967). Evidence of non-depositional episodes was rare, but occasionally spectacular, such as the articulated skull and jaws of a *Protemnodon* (Fig. 4a), found buried slightly nose-down in the middle of the main passage. The front part of the skull was perfectly preserved, but no trace remained of the cranium or back of the lower jaws. Also, an early rockfall seemed to have been cemented with a thin flowstone crust before being buried by later silt.

During later quarry operations lower extensions of the cave were found and excavated by John Barrie (this volume).

The internal geometry of the cave was manifestly important in the distribution of the fossils. It was found, for instance, that there were few (and mostly large) bones in the central zone of the passage, except in the lee of fallen rocks. Hydrodynamic sorting into size classes occurred, and bones were concentrated, apparently by stream flow, in alcoves along the walls or in the lee of boulders. This may also be an effect of the movement of animals that had survived the fall —

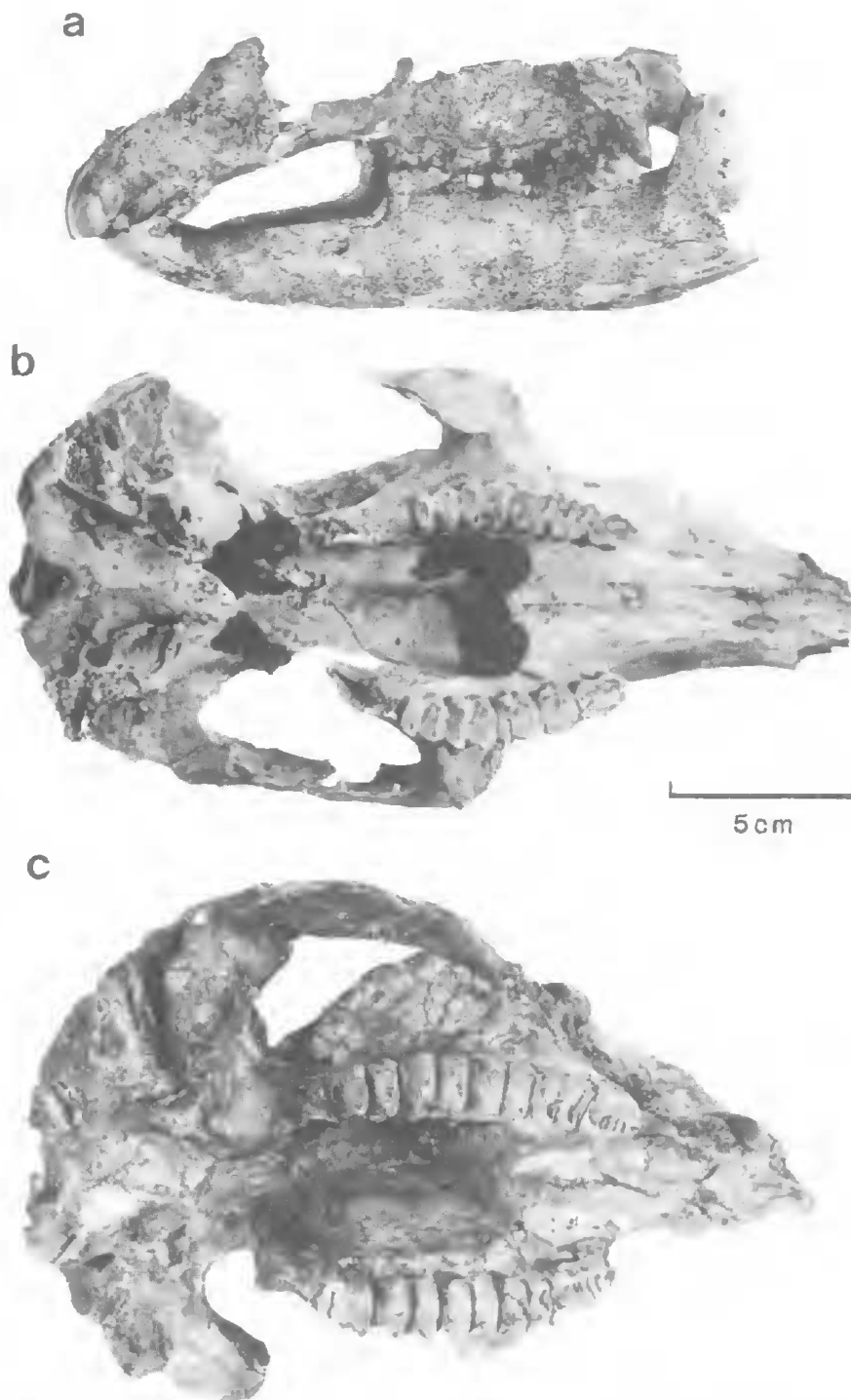


FIG. 4. a) Articulated upper and lower jaws of *Protymnodon roechus* (SAM P22845) showed evidence for erosion which removed all trace of the posterior part of the skull (from Area A2/7). b) Skull of *Sthenurus atlas* SAM P29570 (from Area A10/16). c) Skull of *Simosthenurus occidentalis* SAM P18644, discovered during excavation of the natural entrance shaft. All to same scale. Photos: R. Ruehle.

up to 5 m — into the cave, crushing or kicking aside the remains of earlier victims.

That animals could survive the fall is seen in the partial skeletons of a turtle (*Chelodina*) and a (?) swan found together behind a large rock about 15 m from the pitfall entrance where it is unlikely they would have been washed intact. Many, if not most, remains come from animals that fell into the cave and were trapped, while the few sparse and fragmentary specimens of *Diprotodon* indicate that its remains were washed in from the surrounding hillside. In any case, an adult *Diprotodon* would have stuck in the entrance. There is no convincing evidence that any animal freely inhabited the cave during this last phase of its existence, except possibly during periods when tree trunks or branches had fallen into the entrance to act as ladders. No "fossil" wood has been found, but numerous tubular, branching holes have been interpreted as moulds of twigs, and a large (5 cm diameter) charcoal-lined cavity with a woody-like surface texture presumably represented a charred branch washed in after a bushfire.

Finely disseminated and chunky pieces of charcoal occurred irregularly through the sediment, though very little was found in either the uppermost or lowermost layers. Two aggregated samples were dated by the Radiocarbon Laboratory, University of Sydney (Gillespie & Temple, 1979) as follows:

SUA-140. Area A3, depth 105–120 cm, gave a background result. Age greater than 35,000 years. $\delta C14$: -997.7 ± 4.0 ; and

SUA-234. Area A1, depth 30–75 cm. Age 33,800, $\pm 2,400$ / $-1,850$. $\delta C14$: -985.1 ± 3.9 .

Archer (1974) has shown the difficulties of dating fossils from associated charcoal, and it must be stressed that the above dates should be regarded as indicative rather than definitive, in view of the small charcoal sample sizes obtainable for dating, and the possibility of contamination of far older charcoal.

Extrapolating these charcoal age values suggests a deposition span for this part of the cave system of about 8,000 years, ceasing when the natural

entrance finally became permanently blocked by its own talus pile perhaps 32,000 years ago. Periods of non-deposition may have occurred when the entrance became temporarily blocked. Pondered mud and water from heavy rains would eventually have softened and overcome the obstruction and released a mudflow of debris as described by Wells *et al.* (1984). Evidence of such flows may be interpreted in the jumbled orientations of bones. Such events undoubtedly have caused perturbations in the species abundance charts, but these effects would have been outweighed by other factors affecting the data.

THE FAUNA

The fauna is listed in Tables 1 and 2, together with aggregate totals of the mammals in the volume of census. Note that many fragmentary jaws of smaller taxa were not identified to species level. No attempt was made to estimate numbers of non-mammalian vertebrates.

AMPHIBIA

Tyler (1977) identified and discussed collections of fossil frog ilia from the Victoria Fossil Cave and the Henschke Fossil Cave. Subsequently *Geocrinia laevis* was recognised in further material from the latter cave, but *Limnodynastes* cf. *L. dumerili* is still absent there. There are other notable absences, as discussed by Tyler (*ibid.*).

REPTILIA

Smith (1976) lists twelve reptile species from the Victoria Fossil Cave at Naracoorte: five snakes and seven lizards. Most specimens from the upper Henschke Fossil Cave have not been identified or studied in detail, but there is no reason to expect any significant difference.

There are two notable exceptions, however. The giant python *Wonambi naracoortensis* Smith is not present in the upper part of the Henschke cave system. Barrie, however, reports (this volume) on almost complete material from the lowest levels.

TABLE 1. Faunal List: non-mammal species.

AMPHIBIA: <i>Geocrinia laevis</i> ; <i>Limnodynastes tasmaniensis</i> ; <i>Litoria ewingi</i> ; <i>Ranidella signifero</i>
REPTILIA: <i>Chelodina longicollis</i> ; <i>Amphibolurus</i> spp.; <i>Tiliqua rugosa</i> ; Scincid undet.; <i>Varanus</i> sp. cf. <i>V. gouldii</i> ; <i>Pseudonaja</i> sp.
AVES: <i>Dromaius novaehollandiae</i> ; <i>Progura naracoortensis</i> (extinct); <i>Cygnus</i> (?) sp. or <i>Anseranas</i> n. sp.; <i>Turnix varia</i> ; <i>Hirundo neoxena</i> ; Corvidae undet.

TABLE 2. Faunal List: mammal species, with minimum number of individuals within census areas (A0-A8).

MAMMALS	
SPECIES	AGGREGATE NUMBER OF INDIVIDUALS
<i>Zaglossus ramsayi</i> **	6
<i>Dasyurus viverrinus</i>	54
<i>Antechinus</i> cf. <i>A. minimus</i> } <i>Sminthopsis leucopus</i> }	34
<i>Phascogale</i> sp.	1
<i>Sarcophilus laniarius laniarius</i> **	6
<i>Thylacinus cynocephalus</i> **	12
<i>Perameles</i> cf. <i>P. gunni</i> } <i>Perameles</i> cf. <i>P. bougainville</i> * }	469
<i>Isodon obesulus</i>	96
<i>Phascolorctos</i> cf. <i>P. cinereus</i>	2
<i>Vombatus ursinus</i>	8
<i>Lasiorhinus</i> cf. <i>L. latifrons</i> **	18
<i>Diprotodon optatum</i> **	5 tooth fragments
<i>Zygomaturus trilobus</i> **	3
<i>Petaurus breviceps</i>	2
<i>Pseudocheirus peregrinus</i>	1 tooth
<i>Cercartetus nanus</i>	(1)
<i>Trichosurus vulpecula</i>	(1 tooth)
<i>Thylacoleo carnifex</i> **	46
<i>Propleopus oscillans</i> **	1
<i>Potorous tridactylus</i> } <i>Potorous</i> cf. <i>P. apicalis</i> } <i>Potorous</i> cf. <i>P. platyops</i> * }	280
<i>Bettongia</i> cf. <i>B. gaimardi</i> } <i>Bettongia</i> cf. <i>B. penicillata</i> } <i>Bettongia</i> cf. <i>B. lesueur</i> (?)* }	137
<i>Aepyprymnus rufescens</i>	2
<i>Lagorchestes leporides</i> *	58
<i>Wallabia</i> cf. <i>W. bicolor</i>	5
<i>Macropus</i> cf. <i>M. giganteus/titan</i> **	147
<i>Macropus</i> cf. <i>M. rufogriseus</i> *	335
<i>Protemnodon roechus</i> **	8
<i>Procoptodon</i> cf. <i>P. rapha</i> **	(1)
<i>Sthenurus atlas/andersoni</i> **	16
<i>Simosthenurus gilli</i> **	32
<i>Simosthenurus occidentalis</i> **	12
<i>Simosthenurus brownei</i> **	1
<i>Simosthenurus maddocki</i> **	5
<i>Simosthenurus pales</i> **	6
<i>Nyctophilus</i> cf. <i>N. geoffroyi</i>	1
<i>Mastacomys fuscus</i> } <i>Conilurus</i> * }	114
" <i>Rattus</i> " spp.	224
" <i>Pseudomys</i> " spp.	30
<i>Hydromys chrysogaster</i>	3

*Extinct on mainland

**Totally extinct

Numbers for census volume only (areas A0 to A8)

Figures in parenthesis recorded only outside the area.

Fragments of shell referred to the turtle *Chelodina longicollis* occur widely through the deposit, and an almost complete carapace and plastron were found in a situation suggesting the animal might have survived its fall into the cave. The presence of this species here is interesting, as Smith (1976) does not report turtles from the Victoria Fossil Cave, and Wells *et al.* (1984) only list cf. *Emydura macquarii*. Presumably the turtles migrated up from the marsh and swamp a few hundred metres away to lay their eggs in the sandy slopes of the East Naracoorte Range.

Dermal scutes of *Tiliqua rugosa* and various reptilian vertebrae are locally abundant in the deposit, and jaws of *Tiliqua* sp. indicate it was the most common taxon. The scarcity or absence of varanids and gekkonids suggests that they were able to escape the pitfall trap that held their less scansorial brethren.

AVES

By far the most abundant bird fossils represent the extinct giant mallee lowl *Progura naracoortensis* (van Tets, 1974) which seems to have been more common here than in the Victoria Fossil Cave. This may be because its poor flying ability made it more susceptible to being trapped in the narrow pothole funnel than in the large entrance which Wells delineated (Wells *et al.*, 1984). It is, therefore, rather surprising that there is such limited and fragmentary emu material - enough only to suggest it was derived from scattered surface debris.

Other birds also are rare. The swallow *Hirundo neoxena* probably nested in the entrance and the quail *Turnix varia* may have come from an owl pellet. Both are represented only by a few isolated bones. By contrast, the swan, (?) *Cygnus*, being studied by van Tets, comprises most of the skeleton, and seems to be a new species.

Compared with the Victoria Fossil Cave, with 17 species (van Tets & Smith, 1974) the Henschke Fossil Cave upper fauna is markedly depauperate in birds, with possibly only four species in common. This difference probably reflects a difference in mode of accumulation, for van Tets and Smith postulated a large avian predator component, which is not evident here.

MAMMALIA

MONOTREMATA. Although bones of *Tachyglossus aculeatus* may be present, they have not been distinguished from those of *Zaglossus ramsayi*, the giant long-beaked echidna (Pledge, 1980). Bones

of the latter are widely scattered through the deposit and are locally common, suggesting associated material from a single individual. Two near-complete skulls have been found, but the number of limb bones suggests more individuals were present. Barrie (pers. comm., 1937) has found associated remains, including skulls, of several specimens in the lower levels of the cave.

MARSUPIALIA

DASYURIDAE. The most common dasyurid is *Dasyurus viverrinus*, which is fairly evenly scattered throughout the deposit. As Smith (1972) has noted, it is difficult to distinguish *D. viverrinus* from *D. geoffroyi* without having complete, undamaged palates, but tooth dimensions favour the former species. Species of *Antechinus* and *Sminthopsis* together are almost as common and evenly distributed. Only a few have so far been provisionally identified to species level, but these differ from those listed by Smith (1972). A single jaw, bearing only the canine, is referred to *Phascogale*.

Sarcophilus is notable for its markedly skewed stratigraphic distribution (Fig. 5). Most specimens are within the top 15 cm of the deposit. They are uniformly large and massive, more so than modern comparative material at hand, and should therefore be known as *S. lanarius lanarius* (Werdelin, 1987; see also Dawson, 1982a). Only isolated teeth, some of which may have been misidentified thylacine teeth, were found below 60 cm.

In contrast, *Thylacinus cynocephalus* occurred fairly uniformly, though rarely, throughout the deposit. As most jaws were from young juveniles, the abundance could be greater, because there were numerous isolated teeth that had not developed solid roots or showed signs of wear, and had therefore come from disintegrated juvenile jaws. The collection also includes one of the largest dentaries, of an aged individual, I have seen. It exceeds any modern specimen in the South Australian Museum's collections. However, such size differences are not worthy of specific distinction (Dawson, 1982b).

PERAMELIDAE. Bandicoots are overwhelmingly abundant, particularly in the lower parts of the deposit (though this may be an artefact of hydrodynamic sorting, where they were preserved preferentially in alcoves towards the floor of the tunnel). There is a general decrease in abundance

of both *Perameles* spp. and *Isoodon obesulus* from bottom to top of the deposit. No separation was made of the different *Perameles* species but the larger *P. gunni* seemed to be the more common. Each was more abundant than *Isoodon*. Most specimens were toothless, and frequently broken. Counts were therefore made by pairing only those dentaries retaining the ascending ramus, whether or not they bore teeth. Both species of *Perameles* are now extinct in the Naracoorte area, but *Isoodon* is still found there.

PHASCOLARCTIDAE. Koalas are rare in the deposit, and mostly represented by isolated teeth. The jaws discovered vary slightly from most modern representatives, but the latter are so variable between different wild and zoo populations that they encompass these fossil specimens.

VOMBATIDAE. Most wombats come from the upper 60 cm of the deposit. *Lasiorhinus* is found throughout the sequence but mainly in these top levels, and appears to have coexisted with *Vombatus ursinus* which has a more even distribution. The specific identity of *Lasiorhinus* is uncertain. It differs markedly from the modern *L. latifrons* in having a much larger upper incisor relative to the other teeth. The relative abundance of this presumed open-country animal at the top of the deposit comes as something of a surprise, but coincides with upsurges or reductions of several other species, and must be considered to reflect some major ecological/climatic change around 32,000 years ago. *Lasiorhinus* is not reported from the Victoria Fossil Cave (Wells *et al.*, 1984).

DIPROTODONTIDAE. *Diprotodon* is a very minor component of the cave deposit. Only three fragments of molar, showing the distinctive rugose enamel, and pieces of an upper incisor have been identified. Very poorly preserved vertebrae and limb fragments may pertain to this species, but equally well could belong to *Zygomaturus*. It is apparent that these fragmentary remains were washed piecemeal into the cave from the surrounding hillside. None has been recorded from Victoria Fossil Cave, nor any other cave in the area, but a specimen was collected by E.C. Mais last century during the building of the railway from Mt. Gambier to Millicent, about 100 km from Naracoorte (U.S. National Museum of Natural History specimen, pers. obs., 1972). Another was excavated from a stream deposit near Kingston, SE S.A.

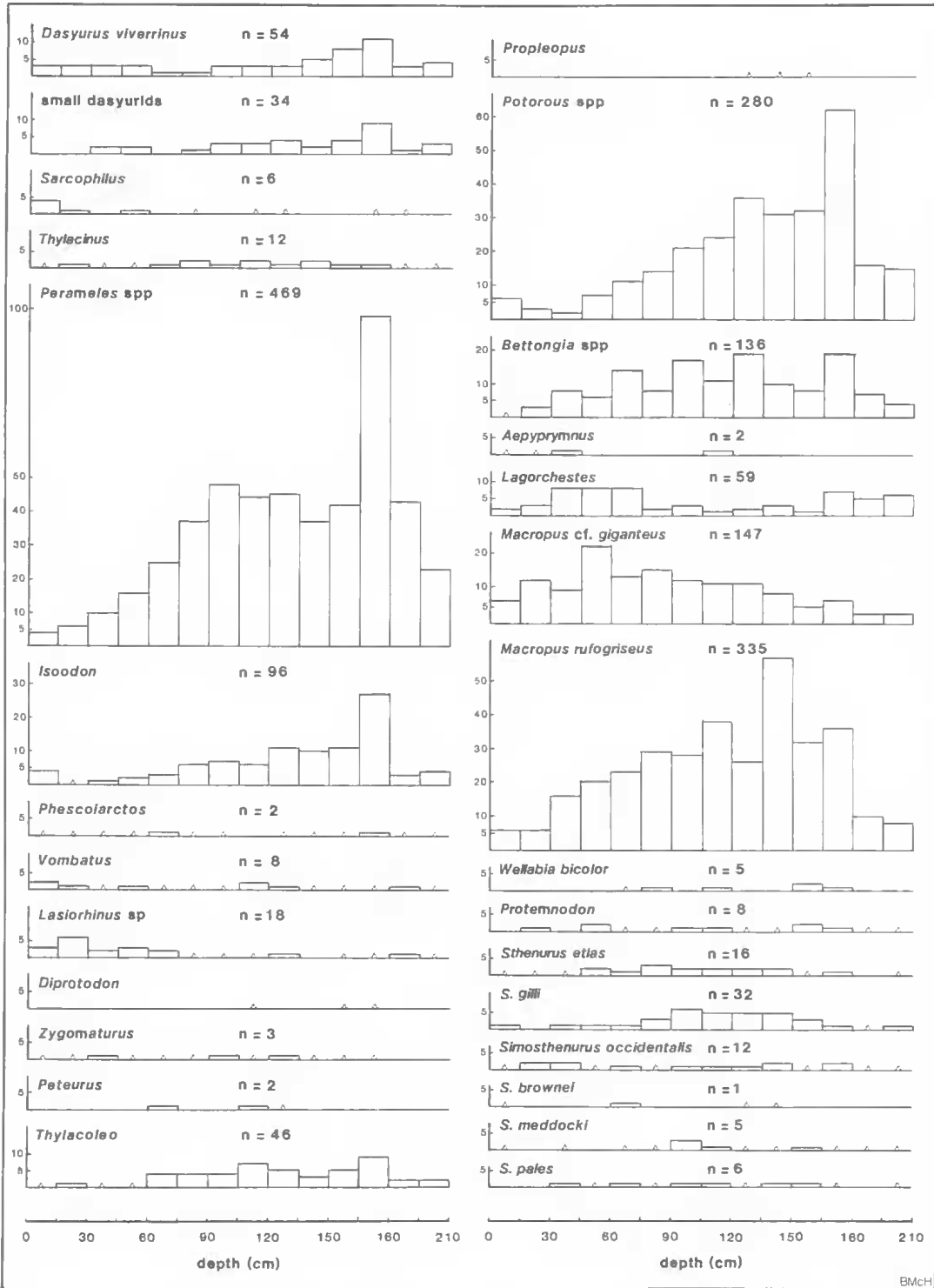


FIG. 5. Absolute abundances with depth of marsupial species in the census areas. Bars represent minimum numbers based on jaws; ticks represent presence of isolated teeth only.

BMCH

By contrast, *Zygomaturus trilobus* is relatively common, being represented by numerous isolated or associated teeth, jaw fragments and some limb bones. Again, however, these remains were probably garnered from the surrounding slope by flash floods, the entrance being too small to accommodate a live animal. This is unlike the Victoria Fossil Cave, where a partial skeleton has been found (pers. obs.).

POSSUMS. The smaller arboreal marsupials are notably rare in the deposit. The Petauridae are represented by two dentaries of *Petaurus breviceps*, the Pseudocheiridae by a solitary lower molar of *Pseudocheirus* cf. *P. peregrinus*, and the Burramyidae by a single dentary of *Cercartetus nanus*. The presence of the phalangerid *Trichosurus* is uncertain as it is based on a single molar. In isolation, such molars are very similar to those of bettongs.

As with the small dasyurids, the rarity of these species is probably best explained by their scansorial abilities, allowing them to escape from the cave. The fragmentary smaller remains may be derived from owl pellets. Smith (1971) records *Pseudocheirus*, *Petaurus* and *Cercartetus* as relatively abundant in the Victoria Fossil Cave, and considers their presence to be the result of predation, possibly by owls. It should be noted that *Pseudocheirus* and *Trichosurus* are particularly common in modern cave deposits in the area.

THYLACOLEONIDAE. The thylacole or marsupial "lion", *Thylacoleo carnifex*, is relatively common for its size and presumed trophic position as top carnivore. It is notable, however, that a large proportion seem to be juvenile, (Fig. 8b) an age distribution seen also in *Thylacinus*. It is considered that this age distribution reflects the inexperience of the young animals, leading them to try to scavenge on animals trapped in the pit — the "baited-trap mechanism".

It must be noted, however, that very few bones bear any sign of the cut marks attributed elsewhere to *Thylacoleo* (cf. Wells *et al.*, 1982). The preponderance of *Thylacoleo* below 60 cm depth probably reflects its ability to climb out of the cave once the silt floor had reached close to the walls of the tube.

POTOROIDAE. Potoroids are almost as abundant as bandicoots. Four genera are recognised, with at least six species. One of the rarest species in this deposit, and in fact countrywide, is the giant musk rat-kangaroo *Propleopus oscillans*. It is known here

from a handful of scattered isolated molars, a premolar, lower incisor and a possible humerus (Pledge, 1981). Barrie (pers. comm., 1987) has found better material in the lower levels of the cave. It has not yet been found in the Victoria Fossil Cave.

Another rare species, known from two fragmentary dentaries, is the rufous rat-kangaroo, *Aepyprymnus rufescens*. This also has not been recorded by Smith (1971) or by Wells *et al.* (1984).

Species of *Potorous* are the most abundant of the potoroids. They include *P. apicalis*, *P. platyops* and *P. tridactylus*, the last of which was not recorded by Smith (1971). Nor did she list *Bettongia* cf. *B. lesueur*, which occurs at Henschke's together with *B. gaimardi* and *B. penicillata*. The uncertainty of identity of *B.* cf. *B. lesueur* is because the otic bullae are not as inflated as in the modern species. No attempt has been made to assign all the material to separate species for census purposes, as much of it is broken and incomplete.

MACROPODIDAE. This family is overwhelmingly dominated by species of *Macropus*, more than half of which have been ascribed to *M. rufogriseus*. These appear to be a larger race than the modern form, being up to 20% larger than specimens from the SE of South Australia. *Macropus* cf. *M. giganteus*, which is only half as abundant, is also about 20% larger than the modern form, but additionally possesses an elongate I³ almost as long as that of *M. titan*. *Macropus titan* has also a greatly enlarged pocket on the rear of the hypolophid of the lower molars, but this is reduced in the Henschke specimens which seem to represent an intermediate form between it and the modern *M. giganteus*. This Pleistocene gigantism has been noted before (e.g. Marshall, 1974). Close relationship between *M. titan* and *M. giganteus* is indicated by Bartholomai (1975). The extinct *M. greyi*, which Wells *et al.* (1984) record as rare, has not been recognised.

Wallabia cf. *W. bicolor* is distinguished primarily by its premolars, which resemble small versions of those of *Protemnodon* (Stirton, 1963). Only five widely scattered jaws retaining premolars were found in this deposit, but others lacking those diagnostic teeth may have been confused with *M. rufogriseus*. *Wallabia bicolor*, which now prefers wet sclerophyll forest, is not found in the region today. Wakefield (1963b) reports it as subfossil from the Portland area of Victoria.

The hare wallaby, *Lagorchestes leporides* is relatively common in the deposit, but its abundance

fluctuates in a manner that does not correspond with any other species. Wells *et al.* (1984) record only its larger sister species, *L. cf. L. conspicillatus*; this is rather surprising as this latter now lives only in northern Australia, whereas *L. leporides* existed in the Murray Basin in historic times (Tedford, 1967).

The giant wallaby, *Protemnodon roechus* Owen, is evenly distributed, although rare, in the deposit. There are a relatively high number of juvenile or immature, suggesting less ability to avoid the pitfall trap. One specimen preserves the articulated upper and lower jaws, complete with incisors, of a mature animal (Fig. 4a). The post-nasal part of the skull had been exposed for some period and removed presumably by "bioerosion" — the passage of other animals during a period of non-deposition.

Associated molars and pieces of maxilla and dentary of a single individual are all the evidence of *Procoptodon* in this deposit, but the specific identity is uncertain. In size and premolar and molar morphology, the specimen agrees with *P. rapha* Owen, but the lower molar tooth row is distinctly curved, unlike illustrated specimens. The dentary of *P. pusio* illustrated by Stirton and Marcus (1966, fig. 6) shows slight curvature of the tooth row, but the molars of this species are noticeably smaller than the Henschke specimen. *Procoptodon rapha*, is recorded from Victoria Fossil Cave (Wells *et al.*, 1984).

The other sthenurine kangaroos, species of *Sthenurus* and *Simosthenurus*, are not common in the fauna, although isolated teeth make them seem so, and their abundance is fairly constant throughout the sequence. Several skulls have been found, despite their fragility. *Sthenurus atlas* (Fig. 4b) and *S. gilli* seem to be slightly more common in the middle part of the sequence; *Simosthenurus occidentalis* (Fig. 4c) is more common towards the top, but with abundances of less than 4% in any one 15 cm interval, this is difficult to prove. Certainly, in absolute numbers, *S. gilli* is most common (Table 2). Because of the often fragmentary nature of the remains, and an apparent variability in tooth morphology, many identifications are uncertain. For instance, Wells *et al.* (1984) listed *S. andersoni* as being more common than *S. atlas*. Direct comparison with some of those specimens, and with Tedford (1966), showed the Henschke material to have characters in common with both species, and intermediate tooth dimensions. Similarly, *S. browni* is listed as more common than *S. occidentalis* in Victoria Fossil Cave, whereas it has been difficult to distinguish in Henschke's. It is notable that the

megadont *S. pales*, not reported by Wells *et al.* (1984), is more common, albeit as fragmentary jaws, than the microdont *S. maddocki* which is reported there.

PLACENTALIA

CHIROPTERA. A single bat jaw has been recovered. Jaw and molar structure are reminiscent of *Nyctophilus geoffroyi*, but this identification requires confirmation. It is obvious that the cave never met requirements for breeding or overwintering, and must at best have been visited only rarely.

RODENTIA. Because of the difficulty of identifying often toothless rodent jaws, no detailed census was undertaken, beyond dividing them into size classes: large (*Mastacomys*, *Conilurus*), "rats" (*Rattus* etc.) and "mice" (*Pseudomys* etc.). In addition, several specimens of *Hydromys* were found. The *Mastacomys* group had fairly uniform relative abundance, increasing slightly towards the top of the deposit. The *Rattus* group initially had an abundance fluctuating between 5% and 10% but rapidly increased in the upper third of the deposit to nearly 30% at the top, while the "*Pseudomys*" group showed low abundance at first, gradually decreasing upwards. The latter trend is perhaps a preservational bias, as protective alcoves were more common and larger at depth, but this does not explain the reverse trend of the *Rattus* group.

POPULATION ANALYSIS

The gross census figures of the marsupials were processed to give relative abundances of species in each 15 cm interval. These figures involve considerable error, in view of the different areal size of each interval, the uncertainty of correlating even adjacent excavation areas, the certainty of frequent reworking of surface layers by flash floods, sheet wash and mudflows (e.g. Archer, 1974), and other taphonomic factors, such as scavenging and biological disturbance.

Despite all these difficulties, however, opposite trends are seen in some species that must reflect external factors of climatic or environmental change. Notable are the distributions of *Perameles* spp., *Isoodon obesulus* and *Potorous* spp. against *Macropus giganteus*, *Lasiorhinus* sp., and *Sarcophilus lanarius*, or *Isoodon* against *Lagorchestes leporides*. These data are shown in Fig. 6.

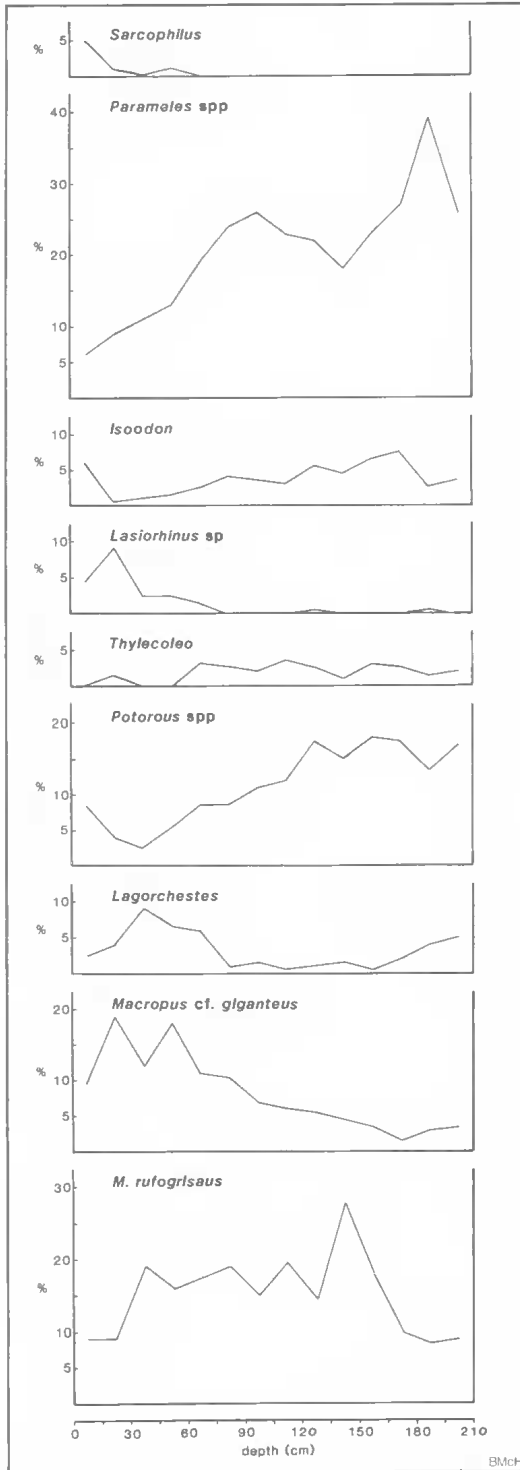


FIG. 6. Relative abundance of selected species, expressed as percentage of total marsupial population of each arbitrary 15 cm layer.

ENVIRONMENTAL ANALYSIS

Wells *et al.* (1984) attempted to relate their deposit on the basis of radiocarbon ages with hydrological and vegetational parameters defined by Bowler *et al.* (1976) and Dodson (1977) respectively. A similar exercise for the Henschke Fossil Cave places the deposit in a wet-drier-wet cycle, with eucalypt forest and dry heath (Fig. 7). More detail is perhaps obtainable by considering the habitat preferences of those species still living. For this purpose, the work of Strahan (1983) has been heavily used. Only species having distinctly non-uniform abundance are considered here (summarised below), as the others apparently were not affected by any climatic/environmental changes.

Dasyurus viverrinus — dry sclerophyll forest, scrub, heathland; forest-grassland mosaic.

Sarcophilus harrissi — sclerophyll forest, coastal scrub.

Vombatus ursinus — forest, woodland, scrub and heathlands, with grass; temperate, humid.

Lasiorhinus spp. — drier open woodlands, scrub and grasslands.

Potorous tridactylus and *P. apicalis* — sclerophyll forest, with thick ground cover, coastal heath, high rainfall.

P. platyops (*P. morgani*) — scrubby woodland, heath (on Kangaroo Island).

Bettongia penicillata — open forest, woodlands, tussock grass understorey.

B. gaimardi — dry sclerophyll forest, grassy understorey, higher rainfall.

B. lesueur — open woodland, grassland, sandy soil, semiarid.

Lagorchestes leporides — open tussock grass plains (Murray Basin).

Macropus rufogriseus — open eucalypt forest with shrubby understorey, tall coastal heath.

M. giganteus — semiarid mallee scrub, forest with open grass, rainfall more than 250 mm.

Hydromys — permanent water.

Conilurus — eucalypt woodland, low hollow branches for nesting.

Mastacomys — alpine to subalpine heathland, open woodland, dense undergrowth in wet sclerophyll forest, sedgeland.

The overall picture is one of scrubby woodland with patches of thick understorey and some open grassy areas becoming larger. Heath may have existed on the lower slopes adjacent to the still existing swamp.

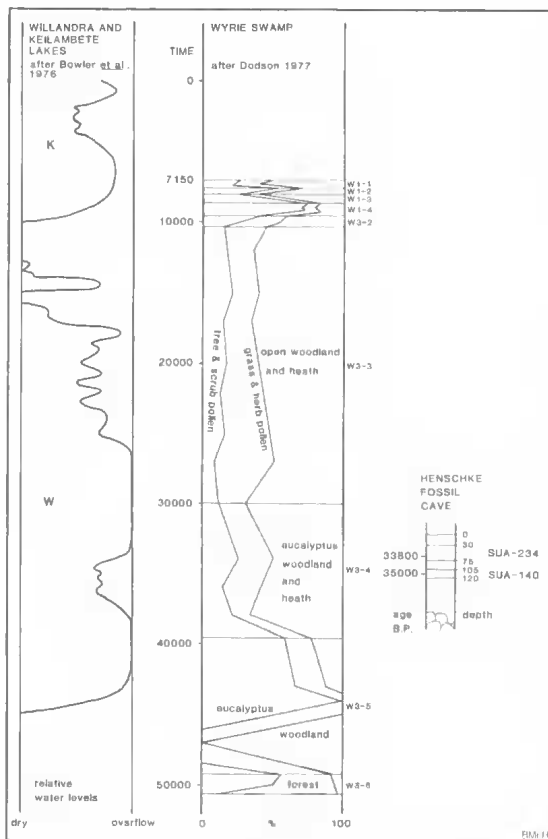


FIG. 7. Henschke Fossil Cave sequence compared with late Quaternary environmental parameters (after Bowler *et al.*, 1976; Dodson, 1977).

DISCUSSION

Comparison of the Henschke fauna (Table 2) with that of the Victoria Cave (Wells *et al.*, 1984) shows a close correspondence in species, with only minor differences, although their relative abundances differ. In contrast, analysis of the Pleistocene mammals in McEachern's Cave (Wakefield, 1967) shows a different, much less diverse faunal composition, with fewer extinct species present. Carbon-dated on bone at 15,200 \pm 320 years B.P. (Gak 509) this fauna may reflect the unfavourable environmental conditions at the end of the Ice Age, despite Wakefield's belief that this was a pluvial period.

Palaeoecological interpretations are fraught with problems arising from the generally undefinable effects of taphonomic processes on the fossils available for study, as well as the ability of some species to survive in less desirable habitats. Wells (1978) has summarised these problems.

Notwithstanding these difficulties, it is considered that the opposing trends and changes of relative abundance shown by certain species reflect actual climatic and/or environmental changes during the filling of the Henschke Fossil Cave. On comparing these habitat preferences, it is apparent that the collection has sampled a mosaic of environmental types, as might be expected of a sandy ridge adjacent to a swampy plain. However, a general trend from wetter, denser vegetation to drier, more open vegetation may be discerned.

Although the age and depth of the dated charcoal samples are of limited value, if they are extrapolated, one obtains an approximate date of about 40,000 years B.P. for the start of deposition in this part of the cave complex, and about 32,000 years B.P. when the cave was finally sealed. This span (Fig. 7) compares favourably with the environmental picture indicated by Bowler *et al.* (1976) and Dodson (1977).

It would seem that at the time of accumulation of fossils in the Henschke Fossil Cave, the East Naracoorte Range was well vegetated with sclerophyll forest and patches of thick undergrowth, but the forest gradually thinned and diminished, to provide more open, grassy areas. Relict patches of dense forest may have persisted nearer the permanent swamp, besides heath and sedge-lands.

The pitfall form of the original cave entrance, as a probably sand funnel-rimmed pot-hole that expanded into a bell-like chamber, argues for catastrophic accumulation of most animals represented in the deposit. However, an arbitrary sample of *M. rufogriseus* jaws (layer 8, i.e. roughly 105-120 cm depth; 49 jaws) was analysed for age structure by determining the stage of eruption of molars. The results are shown in Fig. 8a. Except for the absence of extreme juveniles, the histogram approaches that typical of an attritional mortality sample (e.g. Voorhies, 1969). It suggests that most bones were washed into the cave, or perhaps that a predator had concentrated on one size class — about 15 kg. The absence of very young individuals may be explained by the great fragility of their bones, so that measurable jaws were not preserved. This distribution curve is in contrast to the catastrophic one obtained by Wells *et al.* (1984) for the same species. The only obvious difference in situation is the size and shape of the natural entrance: much larger for the Victoria Fossil Cave, which therefore took a broader sample of the population.

Other departures from the typical attritional curve may be the result of some catastrophic

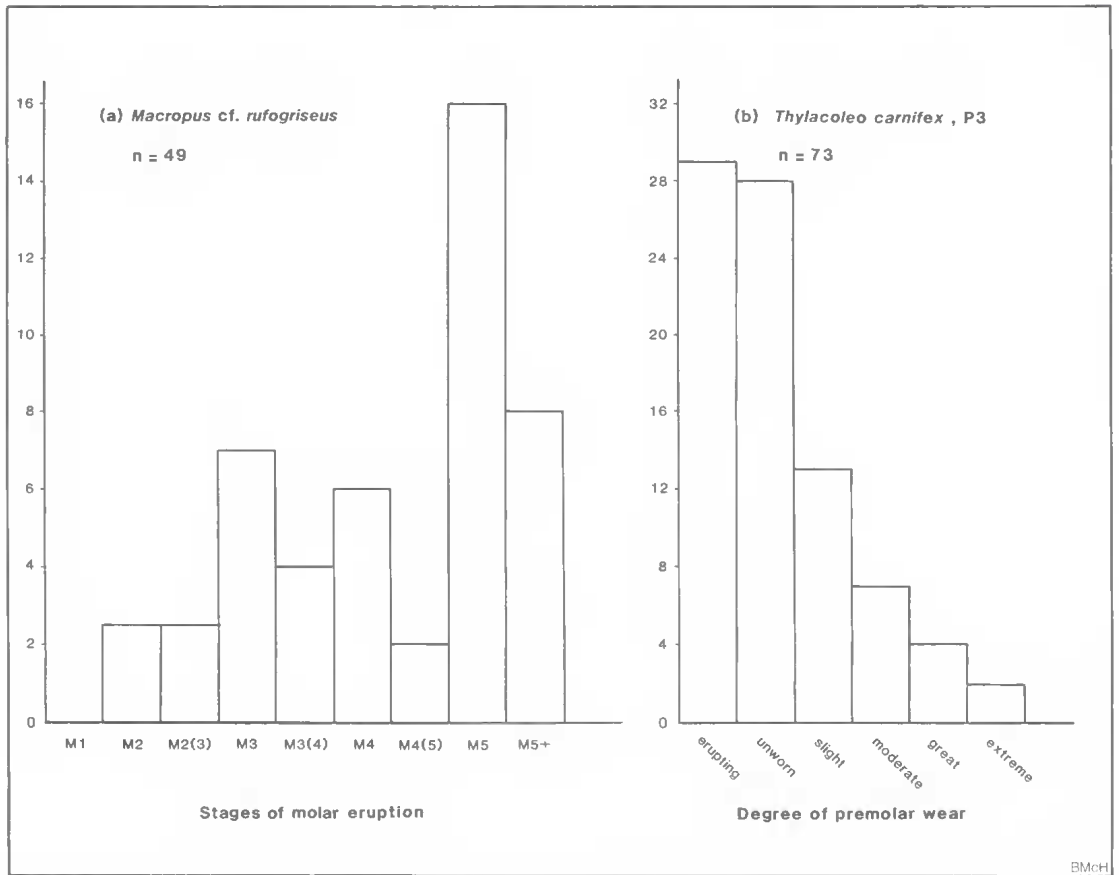


FIG. 8. Age distribution curves of two selected species, based on degree of tooth eruption and/or wear. a) *Macropus cf. M. rufogriseus*, layer 8, minimum number $n = 49$. b) *Thylacoleo carnifex*. Lower premolars P₃, $n = 73$, not corrected for minimum numbers. Total excavated area.

component. There is clear evidence, in the frequent occurrence of charcoal dust and fragments, for occasional bushfires. In such events, animals tend to flee with less care than normally, and would blunder into the pit-fall trap in greater numbers.

By comparison, analysis of *Thylacoleo* ($n = 55$ not corrected for minimum numbers) from throughout the deposit, based on the degree of eruption and wear of the lower premolars, shows a typical catastrophic mortality curve (Voorhies, 1969; Fig. 8b). This suggests that either *Thylacoleo* was attracted to the cave by the sound and smell of dying animals, or *Thylacoleo* was able to use the cave as a den. The latter hypothesis is unlikely except for rare occasions, as when a fallen tree or branch in the entrance shaft could act as a ladder for exit from the cave.

In summary, the presence or, particularly, the absence of a species must be weighed against its known body-size, habits and habitat. Small

scansorial animals may be rare because of their ability to escape the trap, and because there was little predator input into the deposit. Large animals may be rare because they could avoid the relatively small entrance, or because they preferred a more open environment (e.g. *Diprotodon*). Absence of others (e.g. *Palorchestes azael*) may be because of their general rarity in the fauna. Most species samples are the result of a combination of attritional and catastrophic accumulation. Despite reworking of surface material, changes in species abundances indicate environmental changes during a period of about 30,000 to 40,000 years ago.

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